植物研究雑誌
J. Jpn. Bot.
67: 1–9 (1992)

原 著

Structure and Affinities of the Petrified Plants from the Cretaceous of Northern Japan and Saghalien VIII *Parataiwania nihongii* gen. et sp. nov., a Taxodiaceous Cone from the Upper Cretaceous of Hokkaido

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北日本及びサハリンの白亜紀産石化植物Ⅷ スギ科球果の新属新種 *Parataiwania nihongii*

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(Received on May 27, 1991)

A petrified taxodiaceous cone from Ikushumbetsu, Mikasa City, Hokkaido, Japan, is described as a new genus. This cone closely resembles *Taiwania* because it has non-peltate bract-scale complexes with tapered apices and similar vasculature and histology of fundamental tissue, but it differs in having vestigial ligulate scales which *Taiwania* does not.

(Continued from Ohsawa *et al.*, J. Jpn. Bot. **66**: 356-368, 1991)

In the Taxodiaceae, female cones consisting of non-peltate bract-scale complexes with tapered apices are found in *Cunninghamia, Taiwania* and *Athrotaxis selaginoides* Don. Fossils with similar characteristics have been described from the Upper Cretaceous and Tertiary in the Northern Hemisphere; *Cunninghamiostrobus* (Stopes and Fujii 1910, Ogura 1930, Miller 1975, Miller and Crabtree 1989) and *Elatides* (Heer 1876, Harris 1953), are both comparable to *Cunninghamia,* and *Athrotaxites* is close to *Athrotaxis* (Miller and La Pasha 1983). *Sphenolepis* (Schenk 1871, Harris 1953) also has non-peltate complexes with tapered apices, but its closest living affinities are not known. These earlier discoveries show that some degree of diversification had occurred as early as the Late Cretaceous and gave rise to ancestors of some extant genera. However, fossil cones that are attributable to *Taiwania,* have not so far been reported.

Materials and methods

In 1986, Mr. Mitsutoshi Nihongi of Sapporo found a petrified coniferous cone in the riverbed

of the Kumaoizawa River, near the upper reaches of Lake Katsurazawa, Ikushumbetsu, Mikasa City. It was embedded in a calcareous nodule derived from the Late Cretaceous Upper Yezo Group. The geology of the Ikushumbetsu area has been studied extensively by earlier workers, and the age of the fossil-bearing strata is estimated to be Coniacian-Santonian based on associated marine fauna (Matsumoto et al. 1976). The anatomical details of Nihongi's specimen seemed to be *Taiwania*-like (Nishida 1988), and this paper describes its structure regularly. All micropreparations used in this study were made by the cellulose-acetate peel technique using 0.5 N hydrochloric acid as an etching reagent.

Systematic treatment

Order Coniferales

Family Taxodiaceae

Genus **Parataiwania** gen. nov.

Diagnosis of Genus. Fossil conifer cone with internal structure. Ellipsoid cones consisting of non-peltate bract-scale complexes with tapered apices. Four-seeded complexes composed of ligule-like scale and fleshy large bract mostly fused except at terminal portion of scale. Vascular trace from vascular cylinder of cone axis to bract-scale complex single and terete, further divided several times to make ten or more strands arranged horizontally in distal portion of bract. Resin canals at abaxial side of strands and arranged horizontally. Seeds inverted with lateral and distal wings.

Type species. **Parataiwania nihongii,** sp. nov.

Diagnosis of Species. Seed cones ellipsoid, more than 19 helically-arranged bract-scale complexes present in median longisection. Scale minute, reduced ligule-like, completely fused with large fleshy bract except for minute free apex. Pith of cone axis consisting of parenchyma and few scattered thick-walled cells. Vascular tissue composed chiefly of few primary and mostly secondary xylem; the former is endarch – the latter consists of tracheids and rays. Tracheids pitted only on radial walls; bordered pits circular and arranged separately in single row. Rays uniseriate and low, less than 7 cells high. Cortex of thin-walled parenchyma with resin canals. Vascular trace to bract-scale complex terete and collateral with xylem facing adaxial side; divides into three and then into thirteen or more strands arranged in transverse row in distal portion of complex or bract. Scale almost completely fused with bract except for ligulate free apex. Tapered bract constitutes majority of complex. Four inverted seeds surrounded by lateral and distal wings per complex; micropyle towards cone axis. Integument consisting of two layers; outer sclerotic and inner parenchymatous.

Type and deposition. Specimen no. 860202 (holotype) housed in the Laboratory of Phylogenetic Botany, Faculty of Science, Chiba University, Chiba.

Locality. Bed of Kumaoi-zawa River, a rivulet flowing into Lake Katsurazawa, Ikushumbetsu, Mikasa City.

Horizon and age. Upper Yezo Group; Coniacian-Santonian.

Etymology. Generic name *Parataiwania* means similar to *Taiwania*. Specific epithet is dedicated to Mr. M. Nihongi, specimen collector.

Description of Species. The cone is ellipsoid, 22 mm long and 16 mm in maximum width (Fig. 1A). The cone axis is 2.5×3.0 mm in diameter at the basal part of the specimen (Fig. 1A). Nineteen bract-scale complexes are seen in longisection. These are 7–10 mm long, 1–1.2 mm thick and 5–6 mm wide, arranged helically around the cone axis (Fig. 1A).

Cone axis. The pith is about 0.6 mm in diameter and is composed of thin-walled parenchyma and scattered small numbers of thick-

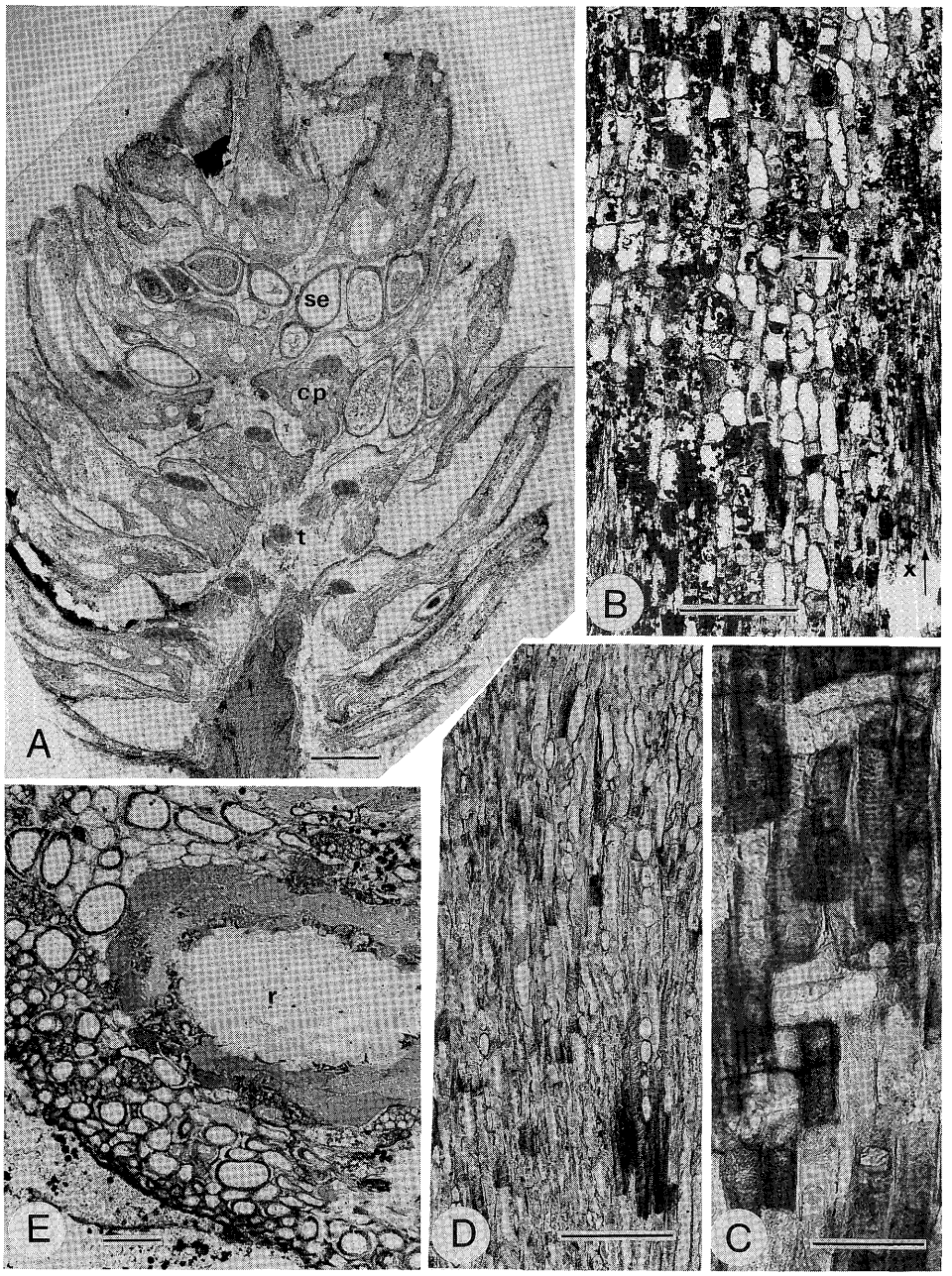

Fig. 1. *Parataiwania nihongii,* sp. nov. A: Longisection of cone. More than 19 bract-scale complexes are visible. se: Seed; four seeds are seen in a bract-scale complex (cp). t: Wedge-shaped vascular trace to bract-scale complex. Bar 2 mm. B: Longisection of pith of cone axis. Parenchymatous tissue with few thick-walled cells (arrow). Left side shows tracheids of primary xylem (arrow x). Bar 100 μm. C: Radial section of secondary xylem of cone axis. Single half-bordered pit in cross field and bordered pits on tracheids are visible. Bar 50 μm. D: Tangential section of secondary xylem of cone axis. Rays of 1–4 cells high are visible. Bar 100 μm. E: Cross section of resin canal (r) encircled by two or three layers of epithelial cells occluded with brown (resinous ?) substance. Bar 100 μm.

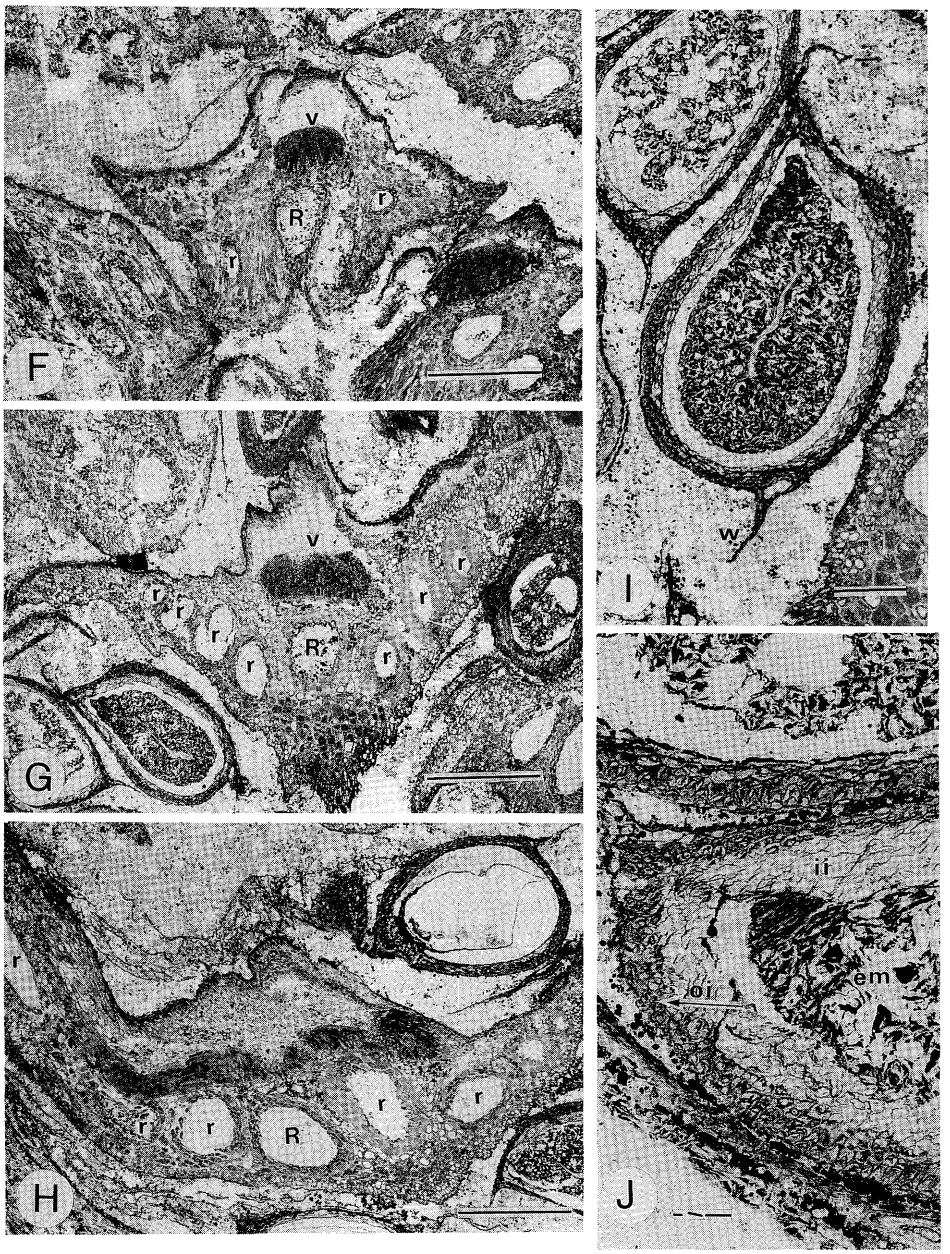

Fig. 2. *Parataiwania nihongii,* sp. nov. F–H: Serial cross sections of bract-scale complexes. Single vascular trace (v in F) divides into three strands (v in G) and then subdivides into several strands (v in H). Resin canals (R and r) increase in number before vascular strands increase. R: Resin canal connects to canal in cortex of cone axis. r: Blind resin canals in complexes. Bar 1mm. I: Seed bearing embryo – obliquely sectioned. w: Lateral wing. A two-layered integument is discernible. Bar 0.3mm. J: Micropylar end of seed. em: Embryo. ii: Inner fleshy layer of integument. Arrow oi: Outer sclerotic layer of integument. Bar 100 μm.

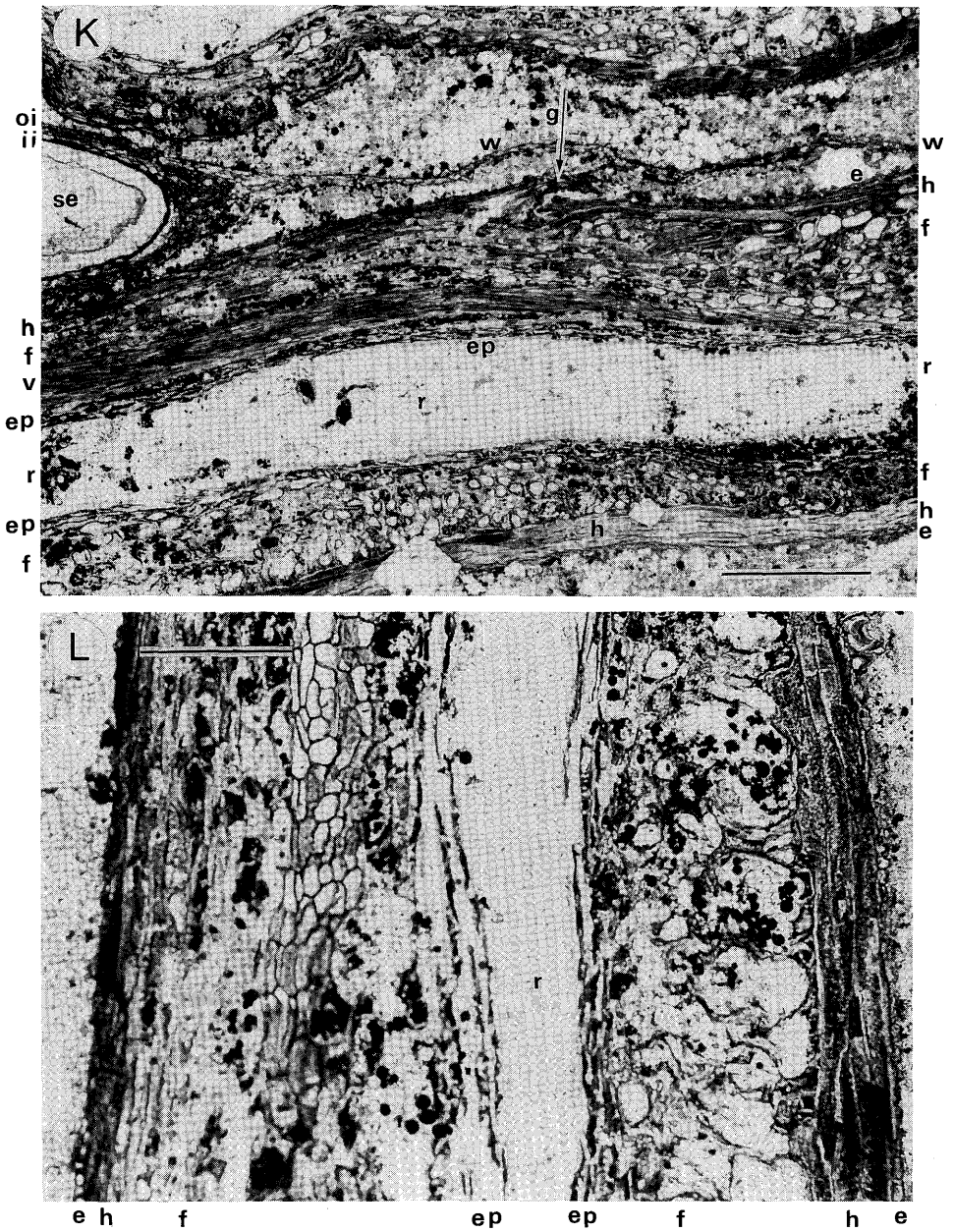

Fig. 3. *Parataiwania nihongii,* sp. nov. K: Longisection of part of bract-scale complex showing lingule-like scale (arrow g), distal wing of seed (w) and tissues in bract-scale complex. Right side is distal. e: Epidermis, ep: Epithelial cells of resin canal, f: Fundamental tissue, g (arrow): Ligule-like scale, h: Hypodermal fibers, ii: Inner parenchymatous layer of integument, oi: Outer sclerotic layer of integument, r: Resin canal, se: Seed, v: Vascular strand, w: Distal wing of seed. Bar 0.5 mm. L: Longisection of part of complex. Legends are the same as those in K. The upside is distal. The vascular strand is not visible in this section. Bar 0.2 mm.

walled cells (Fig. 1B). The pith cells are rectangular in longisection, 40–60 μm in diameter and 40–96 μm in length near the center of the tissue and gradate to cells that are 20–38 μm in diameter and 70–90 μm in length at the periphery. The central cylinder of unknown cross-sectional shape is 0.7–0.8 mm thick at the base of the cone axis and consists mostly of secondary xylem. The primary xylem is endarch, but the number is unknown. The bordered pits on the radial walls of the tracheids are 10–12 μm in diameter and are arranged separately in a single row (Fig. 1C). The rays are sparse, uniseriate, 1–4, and mostly 1–2 (89%), but rarely up to 7 cells high, or 20–160 μm in height (Fig. 1D). The ray cells are ovoid or rectangular in tangential section, 16–28 μm in vertical width and 6–14 μm in transverse width. One or two circular pits, 6–10 μm in diameter, occur in the cross field (Fig. 1C). Secondary phloem is poorly preserved and of unmeasurable thickness. The 500 to 700 μm thick cortex is composed of thick-walled parenchyma. The vascular trace to each bract-scale complex diverges from the vascular bundle of the cone axis as a single thick strand with a wedge-shaped outline in cross section (Fig. 1A, t). The wedge-shaped complex trace extends transversely to the horizontally-stretched bundle (Figs. 2F, 2G).

Bract-scale complex. The bract-scale complexes are 1–1.2 cm long, 5–6 mm thick and 7–10 mm in maximum width. Each complex is falcate-lanceolate in longisectional outline with a tapered apex which is the tip of the bract (Fig. 1A). The complex projects from the cone axis at an adaxial angle of about 60° near the cone base and at an angle of about 45° near the cone apex (Fig. 1A). The complex is composed of a minute vestigial scale and fleshy bract which are fused almost completely (Figs. 1A, 3K). Only the scale tip is free from the bract; it is ligule-like in shape and consists of only four or so layers of cells; one layer each of adaxial and abaxial epidermis and two or so layers of fibrous cells (Fig. 3K; cf. Nishida et al., 1991, Figs. 2, 3). It is 40–60 μm thick and projects for 240–300 μm from the adaxial surface at the distal three-fourths of the bract. Most of the proximal part of the scale where the four ovules occur is fused completely with the bracts (Fig. 1A) which constitutes most of the complex. The bract tissue is composed of one epidermal layer, one or more layers of hypodermis, fundamental tissue (mesophyll), resin canals and vascular bundles (Fig. 3L). Most of the epidermis is eroded and stomata are not discernible. The epidermal cells are rectangular in transverse section and 18–22×8–10 μm in dimensions. The hypodermis consists of 3–7 layers of fibrous cells, 14–30 μm in diameter (Figs. 3K, 3L, h). The fundamental mesophyll is composed of thin-walled parenchyma, 24–86 μm in diameter and a few diffused thick-walled fibrous cells, 40–70 μm in diameter with 14–26 μm thick walls (Figs. 3K, 3L, f). The collateral wedge-shaped complex trace with xylem facing the adaxial side, extends laterally

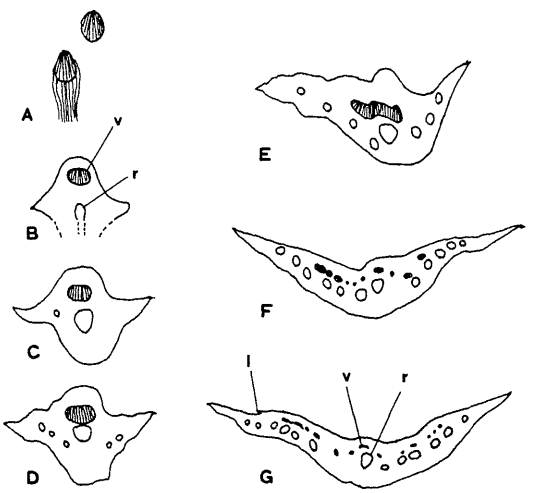

Fig. 4. *Parataiwania nihongii* sp. nov. Semi-diagrammatical figures of serial sections of Bract-scale complex, chiefly showing vasculature. l: ligule-like scale. r: resin canal. v: vascular bundle (xylem only).

as ascends in the bract, divides into three strands and then subdivides into thirteen or more strands in the distal portion (Figs. 2H, 4). Transfusion cells are seen at both lateral sides of the bundles. Three resin canals, one large median canal diverging from the cortical resin canal of the cone axis and two blind laterals are visible at the abaxial side of the vascular trace at the base of the complex (Figs. 2F, 4). More blind lateral canals appear before the increase in the vascular strands ascending towards the distal portion ending in more than thirteen canals (Figs. 2G, 4). They are arranged in an adaxially-facing arc on the abaxial side of the vascular strands and do not subtend each strand.

Resin canals are encircled by two- to three-layered epithelial cells (Figs. 1E, 3K, L).

Seeds. There are four inverted seeds per bract-scale complex, with the micropyle facing the cone axis, and having lateral and distal wide wings (Figs. 1A, 2I, 3K). The integument is composed of two layers: an outer stone layer consisting of sclereids, and an inner fleshy layer consisting of thin-walled cells (Figs. 2I, 2J).

Affinity and discussion. *Parataiwania nihongii* obviously belongs to the Taxodiaceae because it has non-peltate bract-scale complexes with tapered apices, each of which bears more than three ovules and is composed of an almost-completely-fused small scale and large bract. The non-peltate structure with tapered apex of the bract-scale complex is an important characteristic of *Cunninghamia* (Satake 1934), *Taiwania* (Hayata 1907, Sorger 1925, Satake 1934) and *Athrotaxis selaginoides* Don. (Eames 1913) in the Taxodiaceae (Pilger 1926). Although *Sciadopitys* has a similar structure, its complexes are composed of large scales with more than ten vascular strands and small bracts with a single strand (Satake 1934), so it retains pinaceous characteristics (Hayata 1931). *Cunninghamia* has ligule-like scales whose apices are free from the bracts, a single scale trace on the adaxial side of the bract trace, three vascular supplies to the ovules and large bracts with ten or more vascular strands arranged in a horizontal row (Satake 1934). *Parataiwania* resembles *Cunninghamia* in having a ligule-like scale, but differs in the histology of the fundamental tissue and vasculature. *Cunninghamia* has abundant thick-walled fibers, a single scale trace, and three vascular strands which supply the three ovules. By contrast, *Parataiwania* has almost no fibers in the fundamental tissue and lacks specific vascular traces to the scale.

Athrotaxis selaginoides has a completely-fused scale and bract, a few fibers in the fundamental tissue and two or more vascular supplies to the scale (Eames 1913). *Parataiwania* resembles *A. selaginoides* in the histology of the fundamental tissue, but differs from it in having a ligule-like scale.

As described above, *Parataiwania* closely resembles *Taiwania* in the histology of the fundamental tissues of the bract or bract-scale complex and in its vasculature; it has few fibers, a single wedge-shaped vascular trace to the complex, no specific strand for the scale, horizontally-arranged vascular strands in the bract, and resin canals abaxial to the strands. However, *Taiwania* has no ligule-like scale; the bract is really a bract-scale complex (Sorger 1925, Satake 1934). We detected a vestigial minute projection, 240–300 μm long, on the adaxial surface at about the distal three-fourths of the bract in *Parataiwania* by careful examination (Nishida et al. 1991). This projection is liable to be confused with a wound crack in the bract tissue. However, we ascertained by fluorescent microscopy that the cells of the outermost layer encircling the minute projection have cuticular walls which means the projection is

surrounded by epidermal cells and is not a damaged bract tissue but a ligulate-scale apex which is free from the bract (Nishida et al. 1991).

Although *Parataiwania* resembles *Cunninghamia* in having ligule-like scale, it differs from the latter in having almost no fibers in the fundamental tissues of the bract. *Parataiwania* shows the same histology of fundamental tissue as *Taiwania*. Thus, *Parataiwania* has a closer affinity to *Taiwania* than to *Cunninghamia* and is possibly an ancestor of *Taiwania*.

Three genera, *Cunninghamiostrobus, Elatides* and *Sphenolepis,* have been described as ancestral *Cunninghamia* cones. *Cunninghamiostrobus* (Stopes and Fujii 1910, Ogura 1932) from the Upper Cretaceous of Hokkaido seems to really be *Cunninghamia* in histology and morphology. *Elatides* (Heer 1876, Harris 1953) from the Upper Jurassic or Lower Cretaceous of Siberia, Spitzbergen and north Europe has larger scales than those of *Cunninghamia* and also has fibers in the fundamental tissue as in *Cunninghamia* and seems to be a prototype (cf. Harris 1953, p. 36, Fig. 6). *Sphenolepis* (Schenk 1871, Harris 1953) from the Jurassic of Belgium resembles *Athrotaxis selaginoides* in the vasculature, lack of a ligule-like scale, and having fibers in the fundamental tissue (Harris 1953, p. 18, Fig. 3). *Parataiwania* differs from these genera in having no specific vascular strand for the scale, and in having a vestigial ligulate scale and almost no fibers in the fundamental tissue.

We wish to express our hearty thanks to Mr. M. Nihongi for his kindness in offering the specimen. We also thank Dr. Charles N. Miller Jr., University of Montana, USA, for the loan of the micropreparations of *Athrotaxis* cones. This study was supported by two Grants-in-Aid for Scientific Research from the Ministry of Education, Science and Culture, nos. 63540545 and 02640533.

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要 旨

1986年，札幌市の二本木光利氏が三笠市桂沢湖畔，熊追沢で採集したスギ科の球果は，4個の種子を生ずる先細りの果鱗複合体 bract-scale complex が約25個軸上にらせん配列しており，当初から組織学的にタイワンスギ属 *Taiwania* に近縁の新属と推定されていた（Nishida 1988）．標本の保存状態は必ずしも良くはなく，苞鱗 bract 上の長さ240－300 μm，厚さ50－60 μmの小突起が果たして苞鱗の一部が壊れた組織片なのか，またはコウヨウザン属 *Cunninghamia* に見られるような小舌状の種鱗 scale なのか，特定できなかった．最近，蛍光顕微鏡により，小突起がクチクラ層で囲まれていること，即ち表皮により囲まれていることを確かめた．この小突起は苞鱗の一部が壊れた組織ではなく，独立器官，すなわちごく小さな種鱗であることがわかった．この点はコウヨウザン属に似るが，しかし果鱗複合体の基本組織にはコウヨウザン属に見られる繊維が殆どない．この点はタイワンスギ属に近い．結局タイワンスギ属に近縁の1新属（*Parataiwania* と命名）で，タイワンスギ属の原型であると思われる．